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24 February 1978

USSR

TRANSLATIONS ON USSR SCIENCE AND TECHNOLOGY

BIOMEDICAL AND BEHAVIORAL SCIENCES

(FOUO 8/78)

EFFECTS OF NONIONIZING ELECTROMAGNETIC RADIATION

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EFFECTS OF NONIONIZING ELECTROMAGNETIC RADIATION

This serial publication contains abstracts of articles and news items from USSR and Eastern Europe scientific and technical journals on the specific subjects reflected in the table of contents.

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REACTIONS TO UNPERCEIVED STIMULI IN THE PRESENCE OF FUNCTIONAL DISTURBANCES OF SENSE ORGANS

Leningrad SOVREMINNYYE TENDENTSII V NEYROFIZIOLOGII in Russian 1977 pp 68-81

[Article by G. V. Gershuni, Institute of Evolutionary Physiology and Biochemistry imeni I. M. Sechenov, USSR Academy of Sciences, Leningrad]

[Text] In this article, I should like to discuss the functions of human sense organs described by such nonstandard criteria as occurrence of reactions to unperceived stimuli. The appearance of such reactions is very clearly demonstrable in the presence of some pathological states of the central nervous system as well as, as we have established, in healthy individuals who have developed conditioned reactions to stimuli that are below the threshold of sensations of which they are aware.

Studies of this type of phenomenon were conducted by a team of workers at the Physiological Institute imeni I. P. Pavlov, USSR Academy of Sciences, for many years (Gershuni, Alekseyenko et al., 1945; Gershuni, 1947, 1949, 1955). A brief description of this research was published by L. A. Orbeli in 1949. The results obtained had not been summarized to this time. In this article, we shall discuss phenomena observed in the presence of pathology of of the central nervous system occurring as a result of aerial concussion, closed skull trauma and mental trauma.

The onset of marked vegetative and other reactions to stimuli delivered to sense organs, the functional state of which is characterized by the usual clinical methods as partial or total loss of the relevant type of sensibility (auditory, visual, tactile, nociceptive, olfactory, gustatory) is not unexpected. The descriptions of disorders referable to perception of exogenous stimuli, observed in the presence of closed skull trauma and mental trauma (i.e., in the presence of excessive stress for man) of wartime and peacetime, provided by clinicians, have long since indicated this (Veraguth, 1909; Myasishchev, 1929; Panov, 1933; Astvatsaturov, 1935).

What our studies contributed that is new is determined by the introduction of a quantitative evaluation of phenomena, based on the choice and recording of a specific set of reactions, in the first place, and development of measurement procedures for threshold stimuli inducing these reactions, in the

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second place, along with classical methods of determining the thresholds of perceived sensations in response to the same stimuli. By means of these procedures, we were able to establish two quantitative criteria characterizing reactions to unperceived stimuli: 1) The difference between the threshold levels of stimuli inducing this type of reaction and thresholds of perceived sensations.* This difference, which expresses the range of intensity of stimuli that are not perceived, was referred to as the subsensory zone (Figures 1 and 2). We have used the term, subsensory (Gershuni, Alekseyenko, et al., 1945) to refer to the actual reactions that arise to stimuli below the threshold of perceived sensation. 2) Differences in characteristics of reactions arising in response to unperceived and perceived stimuli.

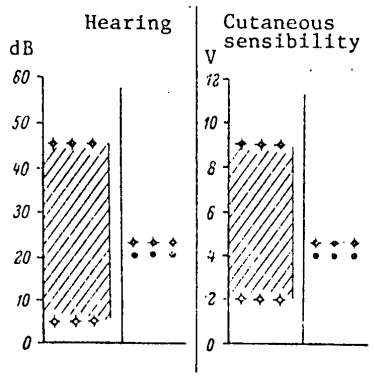

Figure 1.
Thresholds of galvanic skin response (GSR) and thresholds of sensation in patient M. upon sonic and electric stimulation of the skin.
Vertically: intensity of sonic stimulus (dB) in relation to normal hearing threshold (0); intensity of skin stimulation (V) for cutaneous sensibility. White circles--GSR to stimuli below sensation threshold; black circles--sensation thresholds; black circles with crosses--GSR to perceived stimuli. Striped area--range of stimuli that are not perceived (subsensory zone); L--left; R--right.

These criteria enabled us to observe the dynamics of the pathological process in the presence of impaired perception of exogenous stimuli. Thus, at the stage of profound impairment of perception, the difference between threshold levels of stimuli inducing vegetative reactions and thresholds of sensation could reach enormous values, then undergo typical changes in the course of recovery of function. At the same time, we observed typical changes in the characteristics of the reactions.

In order to determine the thresholds of stimuli, in our first work, which dealt with research on functional impairment of sense organs in the presence of wartime trauma (aerial concussion)(Gershuni, Alekseyenko et al., 1945), we used the reaction of dilatation of the pupil, as well as electroencephalographic indices, the change in spontaneous rhythm and initial responses (Gershuni, Klaas et al., 1945). In our subsequent studies, we made extensive use of the galvanic skin response (Gershuni, 1947).

*The term, "perceived (or overt) sensations," is used to refer to phenomena demonstrable in standard psychophysical measurements, as opposed to another group of phenomena referred to, even by I. M. Sechenov, as "sensations in discrete form" (1863).

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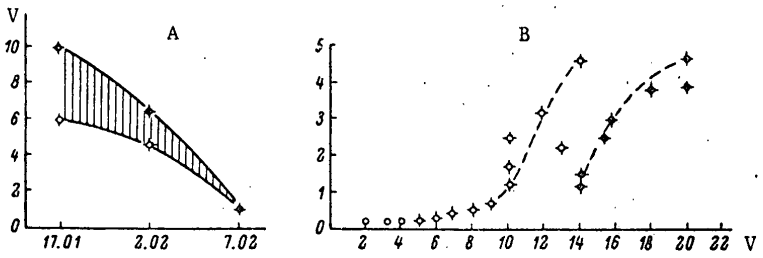

Figure 2. Reduction of subsensory zone and recovery of cutaneous sensibility of patient at the recovery stage (A) and magnitude of GSR as function of intensity of stimuli in and beyond the range of the subsensory zone (B)

In A:
X-axis, day of examination; y-axis, intensity of electric stimulus (V). White circles, GSR to subliminal stimuli; black circles, perception thresholds. Striped area, subsensory zone.

In B:
X-axis, intensity of electric stimulus (V); y-axis, magnitude of GSR (relative units). White circles, stimuli that did not elicit responses; white circles with crosses, GSR to subsensory stimuli; black circles, GSR to perceived stimuli. GSR threshold, 5 V; perception threshold, 14 V

Such vegetative and electroencephalographic reactions were found to be the most sensitive indicators of activity of the central nervous system occurring in response to stimuli that were not perceived.

Figure 1 illustrates a typical case of altered threshold values of stimuli evoking galvanic skin reactions and perception thresholds in a patient with severe, unilateral hypesthesia of the skin and impaired hearing (on the left) as a result of brain concussion. It shows that galvanic skin reactions, to both electrocutaneous and sonic stimuli on the left, arise at threshold levels that are much lower than the perception thresholds for cutaneous and auditory sensations. Upon stimulation of the right side of the body, with normal cutaneous sensibility, the GSR occurs only in response to stimuli that reach the threshold of perceived sensations.

Along with an increase in sensibility as demonstrated by the thresholds of perceived sensations, decrease in subsensory zone until it disappears completely are inherent in recovery of perceptive function in the presence of the above-mentioned disturbances. This phenomenon was demonstrable both in the pupillary reaction test in the course of restoration of hearing (Gershuni, Alekseyenko et al., 1945) and in the GSR in the course of recovery of cutaneous sensibility (see Figure 2A).

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The characteristics of vegetative reactions undergo substantial changes when the stimuli that induce them reach the sensation threshold, i.e., when they begin to be perceived. The most typical of these changes are a reduction in magnitude of reaaction and faster extinction under the influence of successive stimuli. The former phenomenon emerges distinctly when measuring the magnitude of reactions as function of intensity of stimuli that are within and above the subsensory range.

Figure 2B illustrates such data, obtained upon measurement of the galvanic skin response (GSR) as related to intenstiy of electrical stimulation of the skin in a patient with markedly diminished dermal sensibility; the figure shows that when the stimulus reaches the sensation threshold there is a sharp decline of GSR. The entire curve for perceived stimuli is shifted in the direction of higher intensities. Figure 3 illustrates differences in magnitude of GSR and rate of extinction with delivery of stimuli to areas of skin with normal and markedly diminished sensibility.

As can be seen in Figure 3, upon stimulation of the hypesthetic skin area, delivered at intervals of 1 to 1.5 min, GSR of greater amplitude occur throughout the period of stimulation; on the side with normal sensibility, GSR occur only in response to the first stimulus reaching the sensation threshold; there is no reaction to subsequent stimuli.

We should mention one more distinction in the dynamics of effects of unperceived and perceived stimuli; it is referable to increased sensibility (sensitization) under the influence of successive stimuli. This phenomenon, which was studied in healthy individuals by A. I. Bronshteyn (1946), is very marked in patients with impaired dermal sensibility (Figure 4). Figure 4 shows that with successive delivery of stimuli to the skin surface, which induce GSR, the threshold of perceived sensation is reached with the ninth stimulus of very great intensity (3 times greater than the threshold for occurrence of GSR). With continued stimulation, there is a drop by almost 50% of sensation thresholds (sensitization phenomena); accordingly, there is a sharp reduction in the subsensory zone. The thresholds of occurrence of GSR to subsensory stimuli do not undergo apprecialbe changes. Thus, heighted sensibility is inherent expressly in conditions, under which conscious perception of exogenous stimuli occurs.

In different cases of impaired conscious perception, different variants of the above-described phenomena may be observed. The described features of reactions arising to subsensory stimuli, namely, greater amplitude and stability in response to a series of stimuli and lack of dynamics typical of conscious perception (extinction of reactions and sensibilization), are the typical signs that are demonstrable in studies of diverse forms of sensibility (auditory, cutaneous) and different vegetative reactions (pupillary, galvanocutaneous).

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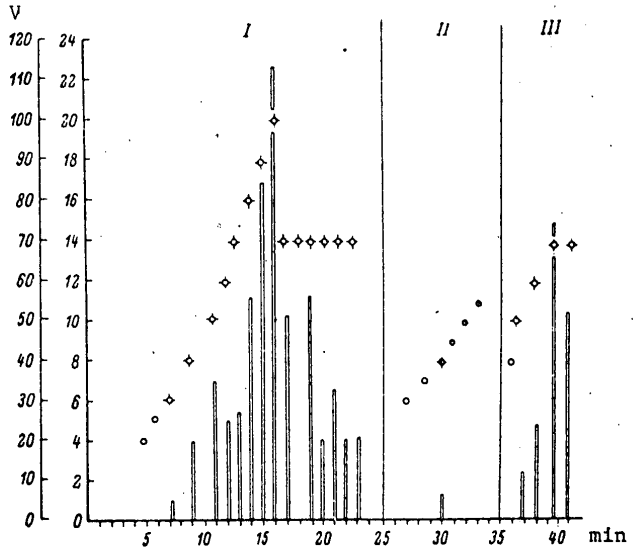

Figure 3. GSR to successive stimulation of anesthetized and normal skin areas

X-axis, time in min; y-axis, intensity of single electric stimuli delivered to the skin (by condenser discharges)(V) and magnitude of GSR (relative units). White circles, unperceived stimuli that do not elicit GSR; white circles with crosses, unperceived stimuli; black circles with crosses, perceived stimuli associated with GSR; black circles, perceived stimuli not associated with GSR. Columns, magnitude of GSR as related to stimuli. Patient So-va (deep anesthesia of both legs, from the toes to the knee). Efferent electrodes on the left hand, silent electrode on the left foot. Stimulating electrode placed as follows: I and III on the lower third of the right leg, anesthetized region; II on the lower third of the thigh on the same side, area of normal sensibility (according to experiments of A. M. Alekseyev and A. A. Arapova).

A comprehensive clinicophysiological description of a group of patients who had sustained air concussion (106 people) was published previously (Gershuni, Alekseyenko et al., 1945). The data illustrated in Figures 1-4 are referable to a group of patients who had sustained closed brain trauma in peacetime (concussion)(studies of Alekseyev and Arapova; Arapova and Orlova; Arapova, Gershuni and Orlova). G. V. Gershuni (1947), A. A. Arapova and G. M. Orlova (1948) published a brief report. All such patients presented impaired perception with severely marked subsensory reactions (22 cases). In a small group of patients (six people), in the history of which the effects of mechanical factors inducing trauma could not be established, similar perception disorders were observed, characterized by marked subsensory

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reactions; the factors inducing these disturbances should have been referred to psychogenic ones (excessive stress for the individual).

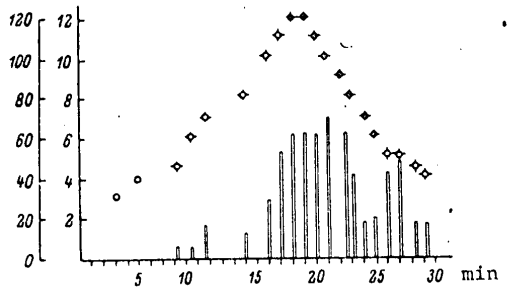

Figure 4.
Sensibilization phenomenon under the successive effects of perceived stimuli. Designations are the same as in Figure 3. The active electrode is on the anesthetized region (lower third of left leg). Patient So-va (Experiments of A. M. Alekseyev and A. A. Arapova)

As we know, in the clinical literature such disturbances were often designated by the term "histerical" or "hysterotraumatic" (Astvatsaturov, 1935). A similar case in wartime was described in 1945 (Gershuni, Alekseyenko et al., 1945). In a work published in 1957 (Avakyan et al., 1957) there is a comprehensive physiological analysis of one peacetime case. Patients with impaired hearing (Kristostur'yan, 1952; Gershuni et al., 1954) and cutaneous sensitivity (Arapova and Orlova, 1948) of peripheral origin were also studied.

In addition, studies were made of patients with impaired cutaneous sensibility as a result of lesions to different levels of the nervous system (syringomyelia, lateral amyotrophic sclerosis, hemorrhages in the region of the pons varolii, comminuted trauma to the right parietal region), but no sensory reactions were demonstrable; the GSR thresholds were found to either coincide or to be above the sensibility threshold. In only one case of a disorder of vascular origin (cerebrovascular thrombosis) with the main focus localized in the right parietal region, accentuated GSR were observed to stimulation of the skin, which were considerably lower than the threshold of perceived sensation. In this case, it was not possible to rule out lesions to other structures, including subcortical ones.

With reference to the above-submitted data as a whole, it should be indicated that the same symptoms, characterized by clinical neurologists (Kryshova, 1945) as subcortical-stem symptoms, are found in patients who have suffered wartime air concussion and peacetime concussion, with which there is typical occurrence of subsensory reactions. The obtained data are inadequate for more precise description of the structures, with injury to which there is typical occurrence of subsensory reactions. The set of phenomena observed with the described disorders of perception is quite typical. It can be described as the syndrome of unconscious [unperceived] perception or, more briefly, the subsensory syndrome.

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In research dealing with the effects of stimuli below the threshold of perceived sensation, in addition to vegetative reactions, electroencephalographic indices were studied. The results of analysis of the electroencephalogram (EEG) and changes therein under the influence of stimuli in patients who had suffered air concussion revealed that spontaneous (background) activity (occipital and temporal leads were used) deviated appreciably from normal and was characterized by the following: 1) instability of the main 8-12-s alpha rhythm, ready disappearance thereof and change to either a faster or slower rhythm; 2) presence of slow waves, of the order of 1-3 per second and spike discharges considerably exceeding the normal EEG variations; 3) impaired electrical activity of the cerebral cortex during sleep (Gershuni, Alekseyenko et al., 1945; Gershuni, Klaas et al., 1945).

The responses to exogenous stimuli (sonic, photic, mechanical, olfactory) are usually manifested by a change in amplitude of dominant EEG rhythm, appearance of relatively fast electric waves and new rhythms at the time the stimuli are used.

In the patient group examined, the reactions to exogenous stimuli were demonstrable with stimuli below the perception threshold. Thus, distinct reactions were demonstrated under the influence of sonic stimuli in individuals who were totally deaf, as well as in response to stimuli delivered to the skin in the presence of severe decrease in tactile and nociceptive sensibility, under the influence of odoriferous substances in cases of total lack of olfaction.

A comprehensive study of reactions to sonic stimulation revealed that the electrical responses are the most distinct at specific times after trauma was sustained. Paradoxical changes were observed in response to relatively mild stimuli and a significant decrease in such changes was found with increase in force of the stimuli. The intensity of the electrical responses diminished in the course of the overall recovery process (Gershuni, Alekseyenko et al., 1945; Gershuni, Klaas et al., 1945).

The subsensory zone could be established from the difference between thresholds of electrical response of the cortex and thresholds of auditory perception, as had been done with respect to thresholds of other reactions (pupillary, galvanocutaneous).

In the patient group studied, the nature of responses to exogenous stimuli presented several distinctions, as compared to the normal findings. In addition to the paradoxical response to mild stimuli, which we have already discussed, the reaction is quite often manifested by intensification, rather than depression, of alpha rhythm, which is very similar to the electric response to exogenous stimuli in the intermediate state between sleeping and waking.

It is significant that, in the course of recovery of different types of sensibility and speech, the stable slow rhythms do not demonstrate a

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correlation to these changes, whereas the reactions to exogenous stimuli change in accordance with recovery of sensibility of a given sense organ.

One of the parameters used for quantitative description of the electrical reaction of the cortex to sonic stimuli was the latency period of such reactions. The latency period was defined as the time that elapsed from the moment sound was delivered to the moment of appearance of EEG changes (accentuation or attenuation of alpha rhythm, accentuation of beta rhythm, appearance of initial response). Shorter latency periods were found in a number of subjects who had sustained air concussion. Increase in the latency period to close to normal levels occurred concurrently with recovery of hearing and speech. Shorter latency periods were not observed in patients with penetrating skull wounds.

Table 1. Latency periods of EEG responses to sonic stimuli

Nature of Disturbance	Subject	Latency period (s)	Mean
Normal	M.	0.23	
	P.	0.45	0.32
	I.	0.29	
	F.	0.29	0.26
Penetrating wound	G.	0.23	
Hearing and speech disorders following air concussion	P.	0.07	
	A.	0.08	0.09
	Z.	0.14	
	T.	0.15	
	I.	0.20	0.12
	V.	0.13	

Table 1 lists mean latency periods for normal individuals, patients with penetrating wounds to the temporoparietal region and patients who suffered air concussion with hearing and speech disorders at the early posttraumatic period. The data referable to latency periods at different stages of recovery of hearing and speech (Table 2) are demonstrative. As can be seen in Table 2, the latency period increased by 3 times during the period, within which hearing and speech are restored.

The EEG data obtained on patients who suffered peacetime concussion presented the same feature in common, appearance of reactions to stimuli below the threshold of conscious perception. To illustrate this, we have submitted in Figure 5 the results of EEG tests on the same patient, whose GSR was studied comprehensively (see Figure 1). This patient has a distinct alpha rhythm. Sonic and cutaneous stimuli (Frey's bristles and hairs) delivered to the hypesthetic half of the body induced subsensory reactions of depression of alpha rhythm. A comparison of these reactions to those occurring in response to stimulation of the other half of the body, with normal cutaneous and auditory sensibility, showed significant differences in

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latency periods and duration of alpha rhythm depression. Thus, the latency period for subsensory sonic stimuli (on the left) is considerably shorter (0.18 s) than upon subliminal (perceptible) stimulation of the right half of the body (0.45 s). The reaction to subsensory stimuli (0.1 s) was found to last much less time than in response to stimuli above the sensibility threshold (2.4 s) with the same physical intensity of these stimuli. The differences in duration of alpha rhythm depression, as can be seen well on the oscillograms, are due to the after-effect, which is several times greater with stimuli that elicit conscious sensations. The phenomenon is equally marked under the influence of both sonic and cutaneous stimuli.

Table 2. Changes in latency periods of EEG responses (according to Gershuni, Klaas et al., 1945) and at different stages of recovery of hearing and speech

Patient	Date examined	Condition of hearing and speech	Latency period(s)
A-v, trauma on 15 Aug 43	19 Sep 43	Hearing and speech absent	0.08
	25 Sep 43	Appearance of hearing at all frequencies on the left, no speech	0.16
	12 Nov 43	Appearance of hearing on the right, speaks in a distinct whisper	0.30
P-f, trauma on 21 Aug 43	14 Sep 43	No speech or hearing	0.07
	15 Oct 43	Appearance of hearing at all frequencies in both ears; stutters	0.12
	22 Oct 43	Speaks more distinctly	0.13
	21 Nov 43	Hearing improved, speaks freely	0.22

The foregoing data characterized perception disturbances that could be demonstrated by specific procedures of psychophysical measurement. These procedures involved the use of simple physical stimuli (for example, pure tones for hearing) and examination of reactions that did not require preliminary experimental development. These conditions facilitated significantly measurement of thresholds and determination of range of stimuli that were not consciously perceived. However, such a study was not sufficient to characterize perception disturbances; in the first place, it was necessary to obtain data on how more complex stimuli, including those used in real life (the sounds of speech, for hearing), are perceived; in the second place, we had to determine the extent to which it is possible to learn to perform specific activity in response to stimuli that are not perceived. Experimentally, this was a question of developing conditioned reactions to subsensory stimuli.

Data pertaining to perception of speech sounds and development of conditioned reactions to subsensory stimuli had already been obtained in the first investigation (Gershuni, Alekseyenko et al., 1945). We submit data below, which pertain to perception of speech sounds described in this work.

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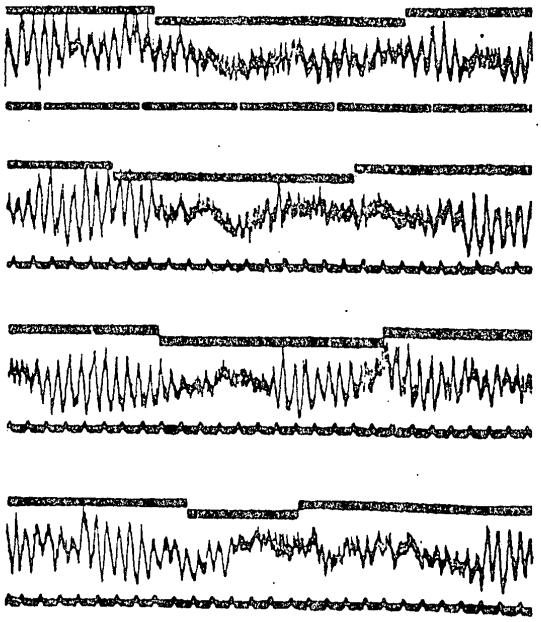

Figure 5. Reactions of depression of alpha rhythm in the EEG of patient M. Left-sided decrease in tactile, nociceptive and auditory sensibility following concussion. Occipital lead.

Top, stimulation mark; bottom, time (1 and 0.2 s). From top to bottom: tactile stimulation of dorsal surface of left arm (subliminal stimulus); tactile stimulation of the same area on the right (supraliminal stimulus); sonic stimulation on the left (1000 Hz; stimulus is 20 dB below sensibility threshold); sonic stimulation on the right, same intensity as on the left (stimulus is 5 dB above threshold)

Perception of speech sounds: Studies of thresholds of auditory sensibility using sinusoidal oscillations of a specific frequency (pure tones) revealed a consistent course of restoration of hearing at different frequencies. In some patients, there was some instability to the degree of decline; however, these fluctuations of threshold did not exceed 10-12 dB. Under specific conditions, speech sound stimuli elicited changes of a very different nature, which could be roughly described as constituting 30-50 dB. The conditions, under which these phenomena could be observed, ensued from consideration of a very interesting procedure for testing hearing, described by L. B. Perel'man (1943) in a study of similar patients. This procedure, which the author called "combined test," is based on concurrent delivery of verbal and

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written signals, fixing the attention on the latter: questions are posed to the patient in writing, and he answers them in writing or verbally (if he can speak). Concurrently with writing the phrase, the experimenter pronounces it at a certain volume; several questions, which follow one another, are written more and more indiscernably. But the subject continues to give the correct answers, and this could only be the result of a reaction to the sounds of speech. We were able to completely corroborate the phenomenon described by L. B. Perel'man, having observed it distinctly in a number of patients (10 out of the 35 studied). By varying the volume of speech sounds, it is possible, in some, cases, to determine how the reaction threshold changes on the basis only of fixing the eyes on the pencil moving along the paper. Of course, this is a rough determination, but this does not diminish its basic significance. Let us consider the two most vivid cases. 1) Patient S-ov lost his hearing and speech after an aerial bomb explosion. At the time of the study, he had regained speech; he had no hearing on the left and could hear loud speech close to the concha on the right. He could respond to relatively low speech, the intensity of which was at least 30-40 dB lower than the level to which he usually reacted, by fixing his eyes on a moving pencil (nothing is written on the paper). The test was repeated many times; each time, fixing the eyes on the pencil elicited a distinct response to low speech. 2) Patient Ya-uk lost his speech and hearing after an aerial bomb explosion. At the time of the study he stuttered. When addressed directly, he could not hear loud speech uttered at close range, near the concha, or the sounds of tuning forks. He could respond to moderately loud speech at a distance of 1 meter when fixing his eyes on a moving pencil, but did not respond to low speech. Thus, fixing the eyes on a moving pencil elicits a reaction to speech sounds, the intensity of which is at least 30 dB lower than the intensity of sounds that are inaudible to the patient when delivered at the concha directly. After 4 days, the patient suddenly began to hear a loud shout near the concha; audiometry revealed a decline of audibility threshold on the order of 100 dB at all frequencies. After 2 more days, he perceived moderately loud speech addressed to him. Audiograms showed typical decline at moderate and high frequencies (of the order of 60 dB).

We shall submit several facts referable to the study of development of conditioned reactions to subsensory stimuli and stimuli beyond this range. We tried to develop conditioned reflexes in response to sonic signals, in the presence of external signs of deafness. In our experiments, we used primarily the method of verbal (written) reinforcement, according to A. G. Ivanov-Smolenskiy. Upon appearance on a screen of the written signal to "depress," the patient squeezed a rubber bulb. A metronome began to tick a few seconds (2-3) prior to appearance of the instruction. Depression of the bulb at the sound of the metronome, before the writing appeared, served as an indication of formation of a conditioned reaction. In several tests we used electric stimulation of the skin rather than verbal reinforcement. The patient had to jerk his hand away from the electrode during passage of current. The clicking metronome preceded delivery of current. Experiments on 29 patients who were totally deaf or had a severe hearing impairment (over 80 dB) revealed that it may not be possible to develop a conditioned reflex in response to the metronome (intensity level of the

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order of 40-50 dB). In this respect, the experimental results were quite similar. As a control, we conducted tests on the same group of patients, using contact with the skin as a stimulus rather than the metronome. Testing of 21 patients revealed that 16 of them could develop a conditioned reflex to tactile stimulation as a result of several combinations. Finally, on another group of patients (15 people) whose hearing had been restored to the extent of perception of the sound of the metronome, the conditioned reflex could be readily formed in 13 cases.

The above facts indicated, on the one hand, that the impossibility of forming conditioned reflexes to inaudible metronome sounds could not be the result of some methodological flaws that generally prevented formation of conditioned associations under our experimental set-up; on the other hand, they showed that conditioned reflexes to sonic stimuli can be readily formed in response to sounds above the audibility threshold.

We altered the experimental set-up to determine the significance of audibility threshold to development of conditioned reactions. Thus, we used a generator of electric oscillations and a telephone as sonic stimuli. We determined the audibility threshold and range of the subsensory zone according to the pupillary reaction at a frequency of 512 Hz. Table 3 illustrates the results of these studies; it contains the typical data obtained on one of the patients who had suffered air concussion. These data show rather clearly that formation of a conditioned motor reflex (movement of the fingers) can be distinctly demonstrated only with sounds that are slightly above the audibility threshold. No conditioned reactions were developed to sounds of considerable intensity, 43 and 50 dB above the threshold for the pupillary dilatation reaction, i.e., stimuli that definitely elicited a flow of afferent impulsation in the acoustic tract.

Table 3. Development of conditioned reflex with the use of different intensities of sound, in patient Sh.

Intensity of sound (512 Hz) above the normal audibility threshold (dB)	Intensity of sound (512 Hz) in relation to patient's audibility threshold (dB)	Formation of conditioned reflex	Number of combinations	Level of conditioned reflex
92	-7	No	30	--
99	0 (threshold)	No	37	--
106	+7	Yes	4	mild
114	+15	Yes	4	strong

The patient had suffered air concussion; he was totally deaf on the left, 80 dB threshold of cochleopupillary reflex; diminished hearing on the right, 100 dB, , 50 dB threshold of cochleopupillary reflex. Subsensory zone, 50 dB. The telephone was put to the right ear.

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The question of development of conditioned reactions to subsensory stimuli in the presence of impaired auditory perception was investigated in greater depth in the subsequent study in our laboratory (Avakyan et al., 1957). The subject (patient M. [female]), who was totally deaf in both ears as a result of mental trauma, was tested many times (18 times) in the course of 1.5 months. She regained her hearing during an experimental session. To test the absolute thresholds, we used the galvanic skin response, which occurred without any preliminary development. This reaction was stereotypically demonstrated in numerous cases; the extinction phenomenon was minimally marked. The threshold intensities at three frequencies (200, 1000 and 4000 Hz) did not differ by over 10-12 dB from the levels considered to be normal, i.e., they were within the normal range according to the criteria adopted in clinical audiometry. Thus, according to the GSR, the subsensory zone involved the entire range of intensity of sonic frequencies used.

We used two types of reactions to develop conditioned reactions to sonic stimuli within the subsensory range: 1) blinking reaction using the method developed by R. V. Avakyan (1955), which permits measurement of absolute and differential thresholds in individuals with normal hearing, during development of conditioned responses to sounds; b) voluntary motor reactions based on verbal or written instructions by the method of A. G. Ivanov-Smolesnkiy (1933). We made mechanical and electromyographic recordings of movements performed in response to appearance of the sign, "lift your finger." Normally, conditioned reactions developed rapidly when appearance of this sign was preceded by an audio signal.

Development of conditioned blinking reactions to sounds, the intensity of which was changed from 90 to 15 dB (i.e., within the subsensory range) was found to be sharply altered, as compared to normal, although it was possible. Formation and particularly fixing of conditioned blinking reflexes in response to low intensities was very slow: about 200 combinations were required for this, i.e., about 20 times more than normally. Even greater differences were observed in development of differentiations, and this was indicative of significant intensification of successive and extinction inhibition.

Unlike the blinking reaction, development of conditioned reflex finger lifting with written reinforcement, just like the conditioned motor reaction of jerking the finger away with electric reinforcement, could not be demonstrated at all. There was rapid development of conditioned motor reactions of this type in this patient, in response to photic stimuli.

The above facts are indicative of the severe perception disorders that can be detected by the conditioned reflex method.

Recovery of hearing, which occurred in this patient during our studies, coincided exactly with the time of appearance of a marked condition reaction of lifting the finger in response to a sound. This phenomenon, which was of particular interest, was detected by the experimenter during a test,

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on the basis of developing reduction of latency periods of motor reactions. Thus, with delivery of the 18th stimulus, the motor reaction recorded on the electromyogram, occurred 0.1 s before appearance of the sign "lift your finger." Thus, we see that there is development of a conditioned motor response to sound. The appearance of distinct, conditioned finger movement, which could not be demonstrated in any of the preceding tests, compelled the experimenter to open the door and enter the chamber, in which the patient was situated. The patient was excited and her face was very flushed; when the experimenter appeared she said: "Last time, I heard something before the sign appeared; before, only the sign appeared. Before this, I felt something like a blow to the head." In answer to the question, "Do you hear me?" the patient exclaimed "I do hear, I hear." She was very excited, tearful and exclaimed "I can hear," and hugged everyone there. The test was interrupted.

Continuation of the study after a break revealed that, with each delivery of the sonic signal there was a conditioned motor reaction, in the form of lifting a finger, and after being instructed by the experimenter to respond verbally to the stimulus, the verbal report of "sound" appeared in response to the stimulus.

A comparison of the signs of restoration of hearing in this patient to the reactions recorded on oscillograms shows that appearance of the first marked conditioned reaction of lifting the finger in response to a sonic stimulus coincides exactly with the same stimulus, with which the patient first reported auditory perception preceding appearance of the sign.

Let us try to evaluate the obtained facts. According to the measurements of absolute thresholds according to the GSR, the sensibility of this patient's auditory system was close to normal. Hence, at sound intensities that were used to develop conditioned motor reactions of finger lifting (50 dB), the flux of afferent impulsation in the auditory tract should have been quite significant. However, this flux could not be used to develop the motor act, which is referable to a complex system of movements referred to as voluntary, in just the same way as for construction of conscious perception of the signal.

However, development of conditioned reactions could occur on the basis of a motor reaction of very specialized significance (blinking reflex); in this case development of the reflex was slow and distorted.

Conclusions

The foregoing indicates that the subsensory syndrome is characterized by rather profound and, at the same time, differentiated disturbances of central nervous system function with complete preservation of afferent flux. Very generally, these disturbances can be described as impaired use of information contained in the afferent flux in specific sensory pathways.

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What facts can we offer to describe the changes that occur in the central nervous system in the presence of the subsensory syndrome: First of all, let us discuss the characteristics of generalized vegetative and electroencephalographic reactions.

The following were typical of vegetative reactions: a) greater amplitude of reactions; b) considerably greater stereotypy of responses in the case of multiple repetition of stimuli.

The following are typical electroencephalographic reactions: 1) shorter latency period and shorter inhibition of alpha rhythm (when this rhythm is pronounced); b) shorter latency period of other reactions (appearance of alpha rhythm in the early responses); c) distorted (accentuated) reactions to mild stimuli.

It should be stressed that the above changes in characteristics of reactions are typical of stimuli in the subsensory range. Such findings are particularly distinct in studies of the process of recovery of perception function. This warrants consideration of the above-described changes as indications of changes in some common elements of the chain of events occurring in the central nervous system, needed for conscious perception of an external signal, as well as for development of conditioned motor reactions related to the system of voluntary movements, rather than concomitant phenomena.

What is the significance of these changes? On this score, several hypotheses can be expounded, which are based on the attempts to interpret the aggregate of observed changes as an expression of impairment of some general biological reactions, in particular, the orienting, waking up reactions, the set of emotional reactions determined by subcortical structures. Very plausible assumptions of this kind were voiced in the work of B. D. Asafov, performed in the laboratory of A. M. Zimkina (Asafov, 1965) and T. N. Reshchikova, performed in the laboratory of E. A. Kostandov (Reshchikova, 1969), as well as Zakharova (1973), in describing subsensory reactions observed in patients with lesions to deep structures of the brain.

It is quite significant that, both in our studies and the above-mentioned, there is a link between the subsensory syndrome and disturbances referable to deep structures of the brain. However, it is not deemed possible at this time, on the basis of the available data, to describe these structures more precisely and, accordingly, to expound hypotheses with sufficient substantiation concerning the role of various regulatory systems in the observed functional disturbance.

However, we could use another approach to this question, which has found experimental expression in the form of studies of formation of conditioned reaction to subsensory stimuli in healthy individuals. It is only after reporting the results of this type of study, with which our team has been concerned for about 10 years, that it is possible to try to discuss the main question, which we can again formulate as follows: How are we to

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interpret the internal correlation between such phenomena as awareness of perception of an exogenous signal (onset of conscious perception) and conditioned motor reactions related to the system of voluntary movements?

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THE ROLE OF ISOLATION, ENVIRONMENTAL DEPRIVATION AND ENRICHMENT IN FORMATION OF BEHAVIOR

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[Article by A. D. Slonim, Institute of Physiology and Experimental Pathology of High Altitudes, Kirgiz Academy of Sciences, Frunze]

[Text] The problem of separating complex forms of behavior into phenotypic and genotypic elements compelled researchers to develop a number of experiments with animals at different stages of postnatal and prenatal ontogenesis. Addition to the environment of new factors, unusual for the organism, or elimination of some of the customary ones were used extensively in recent years to determine the genesis of certain elements (patterns) of reactions of the organism and its systems.

Environmental changes not only have effects based on the plus-minus interaction principle, they also disrupt sharply the entire process of formation of behavior as an integral system. This prompted researchers to investigate the effects of a so-called enriched or deprived environment, as well as to evaluate the significance of this interaction, which occurs in accordance with the feedback principle. Reverse afferentation [feedback], postulated by P. K. Anokhin (1968) as an acceptor of action acquries exceptional importance in many animal species at a specific stage of development, and it is a most important mechanism (for example, in some passerines) that adjusts vocal reactions.

At the same time, elimination of some types of afferentation and reduction of overall information from the environment lead to prevalence of interoceptive influences on the central nervous system and could create a new level of physiological state, sleep. Isolation, with regard to certain types of food, sharply alters some types of appetite (Ugolev, Kassil', 1965) and even leads to energy balance disturbances (Chernigovskiy, 1962).

At the present time, researchers have accumulated considerable material dealing with the effect of isolation and environmental deprivation on the developing organism. These studies can be arbitrarily divided into the following three groups: 1) experiments involving isolation, with regard to some environmental factors; 2) experiments involving isolation of an animal of a given species

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from its usual habitat (and development); 3) experiments involving exclusion of sensory systems (sensory deprivation).

Historically, it happened that the method of isolation of the developing organism from the external environment turned out to be the simplest and, it would appear, most promising method. The history of this method goes back to the legendary experiment of Lycurgus, which has retained its significance to this day.

The famous legislator of ancient Sparta, Lycurgus, took two puppies from the same litter, keeping one of them in a ditch in isolation from the environment and the other under ordinary conditions, among people and animals. When the puppies grew up, they were released to chase a hare. The dog that was raised in isolating hid from fright; the one raised in liberty dashed after the hare and choked it. This experiment served as the basis for education theory, which stipulated that it was imperative to overcome vital difficulties at an early stage of development (childhood) in order to develop positive personality traits in the adult. The experiment of Lycurgus was repeated in the laboratory of I. P. Pavlov, and it was found that the dogs raised in isolation were notable for cowardice and poor adjustment to changing living conditions (Vyrzhikovskiy, Mayorov, 1933).

Isolation may refer to elimination of specific environmental factors, specific types of food, other animals of the same kind, specific forms of activity, physical environmental factors (for example, light), chemical environmental factors (change in air composition), habitat, etc. The isolation method is used at all stages of ontogenesis, but it is particularly important at the early stages of development of an organism, when different forms of behavior and activity are formed.

In the experiment of Cuvier (1842), a young beaver was nursed by a woman. When it switched to plant feed, it would first stack part of the willow twigs in a corner of its cage after having torn the bark off. When some earth was brought into the cage, the little beaver, which had never seen beaver dams, tamped the earth with its tail and stuck the willow twigs into it. Evidently, the experiment of Cuvier is the first reliable experiment on isolated rearing of an animal in order to detect his natural instincts, and it defined the significance of isolation to formation of genetically programmed behavior patterns. This was confirmed by Eibl-Eibesfeldt (1961).

Spalding (1965) kept young swallows in small cages, that precluded any possibility of flying or exercising wing movements. In spite of this, when the swallows were released at the stage of development when they should normally fly, they flew just as well as other birds of the same age.

In the experiments of Grohman (1938), pigeons were kept in cardboard tubes that restricted wing movement. Control pigeons of the same age were able to move their wings without restriction in their nest. The experimental birds were then released from the tubes and their capacity for flying was

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then compared to that of control birds in their first flight. Grohman failed to demonstrate a difference between the two groups.

This experiment showed that the main motor elements of flying in pigeons could develop without prior experience and formation of proprioceptive feedback. However, there was no quantitative evaluation of flying performance. Analysis of fine adaptations developing in the course of exercise is very difficult to make. Petersen et al. (1957) studied development of flying in cabbage butterflies (Pieris). Butterflies that had just emerged from their cocoons were let out from a brightly lit area to determine the height to which they could fly. With age, they ascended higher and higher. Three groups of butterflies were allowed different periods of flying time in order to investigate the role of practicing flying in this refinement. One group was tested from the 1st to 5th day of life, 4 times a day, at 20-min intervals. The second group was kept inactive for the first 4 days, cooling them in darkness to 18°C, then tested just like the first group, on the 5th and 10th days of life. The third group was tested similarly, but was allowed 20 additional "practice" flights before each mandatory test in the first 5 and on the 10th day of life.

Flying characteristics improved with age in all groups, regardless of practice. This improvement was the result of increased rigidity of the wings. The height reached by representatives of all groups of the same age was the same, which rules out the significance of practice. Similar results were obtained in a study of formation of motor activity in an aquatic environment, while swimming.

Carmicheal (1927) restricted tadpole movement that usually takes place in the eggs by submerging them in urethane solution. The tadpoles developing in a motionless state swam quite normally after the anesthetic solution was washed off. Carmichael's data were not completely corroborated by D. A. Sakharov (1957) in the laboratory of Kh. S. Koshtoyants, who observed impaired swimming movements in clean water, after removal of the anesthetic, in frog larvae (Rana pipiens) raised under anesthesia.

Considerable data have also been gathered on formation of specialized reactions in animals using the isolation method. Even L. Morgan (1899) had described a case, when baby squirrels, removed from the nest before they could see, were raised in a room and took nuts, put them on the rug and made "burrowing" movements. After a certain number of such movements, the squirrel would take another nut and repeat the whole procedure.

In studies of the effects of isolation on development of behavior, much attention was devoted to sexual and parental behavior, which are related to preservation of the species. Thus, animals on different phylogenetic levels, which were raised in isolation and encountered the relevant stimuli for the first time, manifested sexual activity. Male leaping spiders go through a very complex courting ritual, which is usually also manifested in specimens raised in isolation (Drees, 1952). True, there are data to the effect that the sexual behavior of guinea pigs is impaired as a result of being raised

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in isolation (Young , 1957): significantly after isolating animals (males) at the age of 2 days and less so when isolated at the age of 10 days (Gerall, 1965). However, according to the data of Harper (1968), when isolated immediately after birth and tested between the ages of 80 and 90 days, the sexual behavior of male and female guinea pigs did not differ from that of control animals. There is reason to believe that these differences are related to the incomplete physical development of animals as a result of ruling out play activity when they are kept alone in opaque cages. This fact confirms our conclusions (Slonim, 1961, 1971) that play is a programmed element of development and has distinct quantitative characteristics referable to specific stages of development (Ponugayeva, 1964, 1968).

Precise quantitative characteristics are very difficult to obtain with regard to the behavior of inexperienced mammalian mothers. For example, rabbits build each successive burrow better than the preceding one (Ross et al., 1956). Such behavioral changes, elicited by activity, are not very noticeable.

A more variegated set of findings is observed in experiments with lower monkeys. Singh (1969) demonstrated that wild specimens of Macaca rhesus and monkeys from Indian temples did not differ from animals raised in partial isolation, with respect to their ability to solve problems in a problem cage. Moreover, the monkeys raised under artificial conditions solved the problems faster than their wild relatives. At the same time, raising Macaca rhesus in isolation led to impairment of "social" and sexual behavior of these animals. In particular, maternal rejection of its offspring and aggressive behavior toward offspring of the same age were observed (Harlow et al., 1971).

This problem, that of development of aggressiveness in isolation, is being worked on very intensively in several laboratories. It was investigated the most systematically on laboratory mice (Valzelli, 1969a, 1969b, 1973), in which a distinctive "isolation syndrome" was described, consisting of several peripheral, behavioral and neurochemical changes in the organism. They include increased muscle tonus, corneal and skin reflexes, piloerection and tremor. There is an increase in spontaneous motor activity, hyperreactivity and development of hypertension. Isolated aggressive mice presented an increase in weight of the adrenals and very accentuated orienting reaction. Progression of these symptoms can be observed when the animals are kept in isolation for 1 to 4 weeks. This effect is observed only in males, since females are not aggressive. Aggressiveness does not develop if over 5 mice are kept in the cage, but it develops to a mild degree when there are 2 and 3 animals per cage. Castration prevents development of aggressive behavior; however, if it had developed prior to this operation, the latter did not eliminate it (Burge, Edwards, 1971). Adrenalectomy attenuates aggressiveness but does not prevent development of the phenomenon (Brain et al., 1971).

The above-described phenomena should be classified as the consequences of "social" isolation, when environmental deprivation involves primarily isolation from specimens of the same species.

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Vocal reactions of animals are another example of the role of experience in development of motor patterns of behavior. In birds, there is a distinct difference between a song, which is a more or less complex sonic expression and calls, which are shorter and simpler sounds. Most calls develop normally in birds raised in isolation from adult specimens of the same species, regardless of whether or not they had heard the sounds of other species. Thus, normal vocal reactions were observed in roosters and chickens raised in an incubator (Schjelderup-Ebbe, 1923). Experiments with small Passeriformes, warblers and black thrushes, raised in isolation, revealed that their calls develop normally (Sauer, 1954; Messmer, Messmer, 1956; Thielcke-Poltz, Thielcke, 1960). The calls were exactly the same as in wild specimens of the same species in all 25 thrushes raised in isolation. The young of many other species of nesting Passeriformes birds were removed from their nest at different times between hatching and acquiring their plumage, and they were hand-fed in varying degrees of isolation from their own and other species. The authors believe that experience in perception of sounds during the period prior to isolation could not have a direct effect on subsequent development of calls, although this possibility cannot be entirely ruled out. The calls of small Passeriformes, skylarks and pied flycatchers (Lanyon, 1957; Curio, 1959), developed normally in almost all cases with isolation. A wild hybrid from a cross between the pied flycatcher and collared flycatcher developed an intermediate call, differing appreciably from the calls of both species (Haartman, Lohrl, 1950; Lohrl, 1950). Consequently, the calls of passerine Passeriformes raised in isolation did not differ from calls of birds in their natural habitat (Miller, 1921; Nice, 1943; Marler, 1956). This confirms the conclusions in old studies involving hand-feeding of nesting birds (Heinroth, 1924) to the effect that, in general, development of interspecific differences in bird calls is relative and unrelated to the acoustic influences of other birds (Stadler, 1929). Normal development of singing was demonstrated in hand-fed baby swallows and sand martins, wrens, pikas, starlings, orioles, reed and corn buntings, as well as bullfinches (in the surveys of Heinroth, 1924; Stadler, 1929; Thorpe, 1961; Marler, 1963). A. N. Promptov (1944, 1956), A. N. Promptov and Ye. V. Lukina (1945) demonstrated the great importance of imitation in development of singing in birds, but the authors also devoted much attention to coordinations in the vocal effector apparatus and differences that arise here. According to A. N. Promptov, vocal reactions as a form of congenital behavior are largely determined by morphological distinctions and function of vocal muscles of the lower larynx. Attention is devoted to both imitation proper, i.e., the capacity for imitation which is congenital, and conditioned reflex changes in focal reactions and motor behavior of birds.

At the present time, it may be considered established that imitation and learning play different roles in formation of vocal reactions (calls and singing) in birds. In this respect, all birds can be divided into three groups (Galambos, Worden, 1972): first group, birds (for example, domestic ones) that retain species-specific vocalization, even if they were deprived of hearing immediately after hatching, i.e., before exposure to calls. This implies the existence of genetically programmed vocal reproduction. In these species, there is no process of comparison of the genetic program

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to acoustic information. The second group refers to birds (passerine Passeriformes) that can develop normal singing, even if raised in isolation; if they are deaf at birth, normal singing does not develop, and this suggests that acoustical feedback (their own voice and singing) plays an important role, apparently in relation to the genetic sound code; the third group of birds refers to those for which not only auditory feedback but an external "model" of species-specific singing must exist for development of voice and singing. For example, in chaffinches raised in isolation singing is impaired, and there are many structures, which are related to imitation in the course of development, that are wanting.

There are very few data concerning voice development in mammals, with the exception of man. Most important is the study of Boutan (1913) of the behavior of a hand-fed gibbon, in whom all 30 studied cries developed normally, although it was not known to what extent this animal was familiar with the sounds of its wild relatives. This question often arises in primate studies. For example, up to 32 different vocal signals can develop in hand-fed chimpanzees (Yerkes, Learned, 1925), but there are no data pertaining to comparison thereof to the calls of wild animals. In spite of persistent attempts to teach lower monkeys new sounds, including human speech, they either failed, or else the results were very insignificant (Furness, 1916; Yerkes, Yerkes, 1929).

Riggs et al. (1972) tried to investigate the effect of lack of hearing on vocalization of adult Saimiri sciureus monkeys. They demonstrated a lack of visible differences in vocalization of normal and hearing-deprived animals. After their birth, the mothers raised their young in an environment deprived of species-specific sounds. One of the offspring was deprived of hearing surgically 5 days after birth. Two others were raised under normal conditions, i.e., they were exposed to species-specific vocalization. Additional data were obtained on 6 other offspring: 4 were raised normally, 2 isolated from their mothers. The sonic spectrograms were studied for 6 months on those raised in isolation and for up to 17 months on the normal ones. Samples of this spectrographic material were analyzed (form of calls and quantitative criteria, i.e., duration, frequency characteristics of squeals and cries). No differences could be demonstrated between experimental and control animals. The sounds emitted by babies and adult animals also failed to differ with regard to these parameters (Winter et al., 1973). Perhaps, there is normal development of vocalization in lower and even higher primates, gibbons and orangutans in isolation.

Seitz (1955) raised a group of raccoon dogs (Nyctereutes procyonoides) in isolation and observed that six calls and variants thereof developed normally; the same was observed in two domestic cats raised in isolation (Weiss, 1952) and in Duplicidentata isolated after the first month of life (Severaid, 1958).

In our laboratory, a large series of studies was conducted at different times on mammals isolated from the environment, related to formation of specialized (species-specific) alimentary and defense reactions.

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In the studies of E. R. Uzhdavini (1958a, 1958b), salivary duct fistulae were created in puppies immediately after birth; he found that, at the age of 20-21 days, the puppies raised on a milk diet presented a positive reaction to meat, consisting of movement toward meat and salivation.

This fact indicates that the inborn reflex to the odor of meat appears in dogs, as in predators, at a specific period of life, at the time when animals switch from milk to a mixed diet. If this reflex is not reinforced with meat, it is extremely unstable and no longer demonstrable at the age of 8-9 months. It is totally replaced by natural conditioned reflexes, which developed in the course of being on a milk diet. Similar findings were made on puppies isolated from their mothers and raised on bottles.

The reaction of newborn Ungulata to shading [dark] above the head, which is particularly vivid on the 1st-3d day of life, disappears when the animal is fed from a bottle, i.e., when this darkness is not reinforced by food (Slonim, 1961). In puppy dogs, a positive reaction to stimulation of the snout with fur is particularly marked on the 2d day, rather than immediately after birth, even if the animals are fed from special droppers. Then, on the 3d-5th day, this reaction disappears, failing to be reinforced by contact with the nursing female.

The studies of A. M. Ugolev (1953) performed with kittens revealed that there is no salivation in response to the sight and odor of meat while they are hunting for live prey, just as is the case in response to the sight and odor of living prey, mice and birds. It was found that this is specific for a predator with the type of nutrition involving stalking of the prey and prolonged tracking thereof; in the kittens that had never hunted, there were the usual, natural conditioned alimentary salivary reflexes, even though they were on a mixed diet. The transformation of kittens into "hunters of prey," i.e., the transition to independent searching for food (feeding on live prey) is associated with an abrupt change in the entire system of unconditioned and conditioned alimentary reflexes. The natural salivary reflexes disappear entirely during the period of stalking the prey or prior to eating, as is the case in adult cats. This unique "transformation" of the kitten into a hunting animal, a predator, occurs at a certain age which, however, fluctuates over a rather wide range.

It was also established that if a kitten, which had not yet hunted for food, is given cut pieces of dead mouse, then a live mouse but with some cuts in it, this transformation can be accelerated due to development of conditioned reflexes to the mouse as a source of food. The abruptness of this transformation in predators is of enormous interest, since it permits determination of the direct effect of the environment on rate of formation of unconditioned reflexes, which are thus far from absolutely independent of environmental factors that have immediate biological significance.

However, the isolated maintenance of kittens in many homes does not prevent them from changing into predators and catching mice and rats; consequently,

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neither imitation nor development of special reflexes determine formation of the predator reaction to live prey. According to the data of A. M. Ugolev, in cats that do not hunt for mice, there is no inhibition of salivation at the sight and odor of food and live prey, which they had never caught.

Formation of alimentary reflexes in predators was confirmed in a newborn lion cub raised on a milk diet to the age of 50 days. It was found that, starting at the age of 30-31 days, it developed a stable, positive motor reaction, without extinction, to the sight and odor of meat. It appeared concurrently with an eye movement reaction to a moving object. Consequently, inborn reactions to meat develop independently of feeding conditions (Uzhdavini, Shepeleva, 1966).

In the studies of A. I. Shcheglova (1959, 1961), young rodents were nursed by their mothers or females of another species: an albino rat nursed a great gerbil, a great gerbil nursed an albino rat, a gray rat nursed a gerbil, etc. In a special series of experiments, a group of gerbils and rats was raised in a warm bag and fed milk from a piece of cotton and a dropper. The animals were tested, starting on their 2d day of life, for 10 min in a special chamber, which contained a digging object, i.e., dry roasted sand, and gnawing objects, wooden sticks. It was found that gnawing and digging began and developed in all gerbils at the same time, regardless of whether they had been nursed by a gerbil, white rat or with a dropper. Digging activity was much less marked in the gray rat than the great gerbil. It appeared on the 18th-19th day of life; gnawing was observed on the 22d day and burrowing on the 14th day. All these reactions developed at the above-mentioned times, regardless of conditions under which the animals were reared.

In the experiments of A. G. Ponugayeva (1960) who studied the milk-hoarding reaction in young golden hamsters, the offspring were raised with their mother but fed a liquid mixture that these animals could not store. In another series of experiments, young golden hamsters were taken from the mother on the 24th day and also fed a liquid diet. These experiments revealed that formation of the feed-storing reaction in the golden hamster is unrelated to rearing conditions.

However, by far not all alimentary reactions develop in isolation, as was shown in the above examples. K. Rakhimov (1958, 1959) found that there was no attempt to graze by hungry lambs and kids raised up to the age of 5 months on a milk diet in strict isolation from others of their species, as well as from pasturage and rought plant feed, when out in pasture. They developed the ability to graze only after being with the herd for a few days. The act of grazing, which is in essence a conditioned reflex, is formed in the nature of an imitation reflex. It is important to mention this, since V. I. Klimova (1956, 1958) established that neonate rabbits, kept on a milk diet, presented an inborn reaction to green feed. The numerous experiments of K. Rakhimov failed to demonstrate this unconditioned reflex to feed of plant origin at any of the phases of development of neonate Ungulata raised on a milk diet. These differences in formation of

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unconditioned alimentary reflexes in rabbits and ungulates could be related to the difference in ecological conditions under which the young develop, a burrow for the rabbits and herd for the ungulates, with the enormous opportunities for forming behavior based on imitation.

The above material warrants the conclusion and the isolation method is, so to speak, the antithesis of the method of development of artificial conditioned reflexes and experimental elimination of some forms of conditioned reflex activity. This route of research, largely substantiated by I. P. Pavlov, presents difficulties, with respect to interpretation of the results, since it requires mandatory comparison to development of inborn behavior.

All of the studies lead to the same conclusion, that the alimentary act and associated salivation reaction are stimulated by the sight and odor of food, and that these reflexes should be referred to the natural conditioned reflexes. If an animal is denied the food inherent in adult specimens of its species from the day it is born, these reflexes are not manifested. Thus, we also find an explanation for the numerous findings of disappearance of predator's reflexes when raised with other species (for example, wolf cubs and lambs, etc.).

However, when interpreting these facts, it is imperative to bear in mind that the transition from milk to a mixed diet, then to independent feeding occurs within specific ontogenetic time frames, and that it is possible to demonstrate the appearance of specialized reflexes to specific foods only in these periods of development of an animal (Kossobutskiy, 1951; Ugolev, 1953; Slonim, 1955; Klimova, 1956, 1958; Rakhimov, 1958, 1959; Uzdavini, 1958a, b, and many others).

With reference to the results of experiments involving isolation from some types of food, we cannot fail to call attention to the fact that appearance and disappearance of a positive reflex to the odor of food is inherent in the ontogenetic process. In these experiments, it is difficult to imagine (in spite of all the precautions taken by the authors: isolated feeding, special uniforms for the service personnel, etc.) that there was total elimination of odors of meat, which had never been reinforced and therefore became an inhibitory stimulus. A special experiment conducted in our laboratory with puppies kept in the vivarium building but in separate cages where olfactory stimuli referable to the odor of meat were not ruled out, and where they were kept on a diet of milk alone, confirmed this thesis. Such puppies did not differ in any way from those kept on a milk diet in an isolated dog house.

This is indicative of the special role of formation of inhibitory conditioned reflexes when using the isolation method. Isolation from different environmental factors not only precludes the possibility of development of natural conditioned reflexes in response to signal-value components of these factors, but could lead to formation of inhibitory reflexes, to development of signs of habituation. This applies, first of all, to olfactory and sonic stimuli, the sensibility thresholds for which are exceptionally high in many animals.

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Disruption of the living stereotype is the second circumstance that is rather important to evaluation of the results of such research. Expressly exposure to a stimulus that was never used before leads to inhibition of reflex activity. For this reason, for example, slow eating of meat by "milk" puppies and lack of physiological reactions adequate to this can be interpreted as the influence of a new alimentary stimulus, unusual for the animal.

Finally, use of the isolation method compels us to pay attention to the fact that isolation from environmental factors and impoverishment of the latter affect not only formation of certain natural conditioned reflexes, but the entire dynamics of cortical processes. This thesis gained experimental confirmation in the studies of staff members of the University of California (Rosenzweig et al., 1972). Studies were pursued of a number of changes in the brain (occipital cortex) of rats kept in an "enriched" and "deprived" environment for 25 to 100 days. The authors proceeded from the fact that, in the laboratory, 3 rats are usually kept per cage. In the "deprived environment," only one rat was kept in each cage. In the "enriched environment," 12 rats were kept together in a large cage that contained toys which were changed daily. Food and drink were available in abundance in all of the cages. Biochemical, histochemical and morphological changes were demonstrated in the occipital cortex of rats from the "deprived" and "enriched" environment. Almost all of the changes were reliable. We were impressed by the sharp increase in thickness of the occipital cortex of "enriched" rats, as well as the increase in number of anatomical synaptic connections per unit area (by 50%) and decrease in their size.

A team of Czech physiologists conducted a large series of studies of this type; they "impoverished" not only the external environment but the diet, and in particular its protein component. Animals raised on a low-protein diet revealed slower myelinization of nerve fibers, development of pyramidal neurons in the sensomotor cortex, an increase in latency period of optical and acoustical evoked potentials (Myslivecek, 1970; Safanda et al., 1971; Myslivecek et al., 1974). Thus, a wide range of phenomena related to nutrition, on the one hand, and delivery of stimuli from the environment, on the other, was demonstrated. It is important to note that both endogenous and exogenous influences determine not only general development of the organism, but primarily formation of the central nervous system, i.e., the brain.

If we scrutinize the method of isolation in detail, in connection with the study of ontogenetic development of functions, we cannot overlook the influence of afferentation on the genetically predetermined process of development. In this respect, it does not matter whether these influences are considered from the standpoint of action acceptor or construction of some other system with feedback. Experimental research involving elimination of different analyzers during the period of postnatal ontogenesis enables us to investigate this question and detect disturbances in the natural course of development, which occur with any form of isolation or restriction of conditions inherent in a given species. In this regard, some interesting data

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are given in the survey of Fox (1970). Fox et al. (1968), having deprived a dog of sight, found normal development and myelinization of the visual cortex, i.e., maturation thereof regardless of control and stimulation. In the in vitro studies of Crain et al. (1970), they demonstrated that blocking agents of the curare type did not affect development of nerve tissue; there was normal development of bioelectric activity at the usual rate. It may be assumed that self-stimulation via proprioceptive feedback after a single movement or during continuous activity of embryos may be significant for normal development of effectors, i.e., the skeletomuscular system, rather than for organization of motor acts. Evidently, this feedback develops after spontaneous mobility is demonstrated, when reflex or evoked activity can be elicited by mild (cutaneous) or more profound (proprioceptive) external stimulation of the embryo. After this phase of effector-affector integration on the segmental level of the spinal cord, there is subsequent integration on higher levels of the developing nervous system until complex coordinated action appears. Hamburger (1963) discussed the possible role of these phenomena in embryogenesis of activity of chickens. Experiments conducted in his laboratory (Hamburger et al., 1965) revealed that spontaneous activity develops before evoked activity, even in isolated segments of the locomotor system, and that extensive generalization, involving the entire nervous system and observed in normally developing mammals after birth, appears on about the 17th day of incubation (Volokhov, 1951; Voyno-Yasenetskiy, 1974; Fox, 1966).

Held and Hein (1963) showed convincingly that deprivation of kittens of all nonvisual sensibility impairs severely their subsequent exploratory behavior that is controlled by sight. Rats blinded at an early age were notable for poor spatial auditory discrimination, as compared to those that had the experience of vision (Spigelman, Bryden, 1967); but rats deprived of sight at an even earlier age coped well with simple problems of auditory discrimination. On the basis of these comparisons, Fox concludes that it is difficult to separate the role of maturation processes from influences of prior experience in development of a specific branch of the nervous system or behavior pattern. In such cases, experiments involving isolation or restriction often induce effects in the form of excessive excitation after isolation and lead to paradoxical phenomena. Thus, Lindsley et al. (1964) discovered that monkeys raised in darkness reacted to light just like monkeys raised under normal conditions react to the light being switched off. Increased excitation in dogs after isolation disrupts their ability to solve problems (Fox, Stelzner, 1966) and to respond to nociceptive stimuli (Melzack, Scott, 1957). Other "nonspecific" influences that could distort efforts to examine a given sensory system or behavior pattern include masking or depression of certain responses due to lack of conditioning or reinforcement; these responses may simply disappear or become "overmature," or else they may be related to unusual stimuli. Kovach and Kling (1967), for example, found that kittens fed from a pipette subsequently refused to suckle their mother. Isolation may disrupt not only maturation of a specific branch of the nervous system (or behavior pattern), but structural and functional integration of one system (or element of interaction) with another. For example, Held and Bauer (1967), Hein and

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and Held (1967) showed that if a collar is put on the neck of a newborn monkey or kitten, which prevented them from seeing their forelegs, it retarded development of association of the eye and front limbs and, after the color was removed, there was no sight-controlled movement of these limbs. Thus, some adjustments must be made to the isolation method. However, for the time being, it is the only means of eliminating learning and memory phenomena and thereby of separating genetically heterogeneous elements of complex behavior of an organism into different stages of formation of functional correlations.

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